Aspen, adaptation, and climate change. Is Alberta aspen adapted to a fossil climate?

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Abstract

Trembling aspen (*Populus tremuloides* Michx.) is very widely distributed throughout North America. It is the predominant early successional tree species of the boreal forest. The species occurs throughout Alberta. It is small and shrubby in the dryer southeastern half of the province, but reaches full tree stature in the mixedwood forests of the north and west of the province. In these areas it is an important fibre source for pulp and oriented stand board production. Aspen is also an important species for wildlife, from beavers to bears, insects and birds.

Aspen re-colonized the bare land surface of Alberta following the retreat of the Wisconsin glaciers about 12,000 years before present (BP). During the hypsithermal 10,000-8,000 BP the climate was warmer and moister than it is now. Since then, there has been progressive cooling and drying, so that current conditions are not as good for effective seedling regeneration. Aspen is also shade intolerant, and its seedlings are very sensitive to competition from pre-existing vegetation; it has been able to persist and spread largely because of its ability to reproduce asexually through root suckers. Following natural disturbance through agencies such as fire, windthrow, or insect defoliation, aspen has re-established itself as the dominant tree species in the early successional stages of mixedwood formations largely through asexual reproduction from remnant roots.

The hypothesis presented here is that aspen is maladapted to current climatic conditions. This is because there has been relatively little opportunity for selection and adaptation to occur among the first colonizers after the retreat of the continental ice sheet in the absence of large-scale regeneration following sexual recombination. It is proposed that, in this part of its range, aspen is adapted to a fossil climate, and that this adaptational lag could become more severe in the event of further climate change.

Alberta aspens do flower and produce fertile seed, so the opportunity for genetic recombination exists. However, the frequency of successful sexual reproduction and stand regeneration events has probably been very much lower in aspen than in other boreal species such as balsam poplar (*Populus balsamifera* L.) or white birch (*Betula papyrifera* Marsh.) where successful sexual reproduction is more prevalent. This might provide an empirical test for the maladaptation hypothesis, since we would expect to find better local adaptation in species that have undergone a larger number of cycles of genetic recombination and selection in the presence of environmental challenges in a changing climate.
Range-wide provenance testing should provide some of the answers regarding the degree of local adaptation in aspen. Such trials would have the added benefit of guiding improved seed transfer guidelines, and they might also point to optimal seed sources for growth under current environmental conditions. Provenance testing should cover both the Canadian and American portions of this species range.

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Introduction

Trembling aspen (*Populus tremuloides* Michaux) has the widest natural range of any North American tree species. It is distributed from Newfoundland to Alaska in the Boreal forests of northern Canada and southwards to Mexico as a montane species in the Rocky Mountains. The species occurs throughout Alberta, where it is small and shrubby in the dryer southeastern half of the province but reaches full tree stature in the mixedwood forests of the north and west of the province. In these areas it is an important fibre source for pulp and oriented stand board production. Aspen is also an important species for wildlife, from beavers to bears, insects and birds.

Aspen reproduction

Aspen reproduces sexually through seed. The seed is very small (5 - 8,000,000 per kg) and it is wind dispersed (USDA Forest Service, 1974). The seed does not usually remain viable for more than a few weeks under natural conditions. While, long-range seed dispersal is possible, the necessary conditions for seedling germination are exacting. Aspen seedlings need adequate moisture for germination and are largely intolerant of competition from established vegetation. Several authors suggest that in the western part of the species range there is essentially no modern seed-based regeneration (Barnes, 1966, Campbell, 1984, Jelinski and Cheliak 1992) largely because it is too dry.

Aspen stands regenerate prolifically following disturbance (particularly fire) through the production of root suckers. The genetically identical ramets thus produced typically form a clone patch numbering tens, hundreds, or thousands of individuals. The size and age of clone patches varies with the frequency and severity of natural disturbance events. In general clone patches are smaller in the northern part of the species range which largely coincides with the extent of the Laurentide and Cordilleran ice sheets. In some more southerly populations the clone patches can number over 47,000 individuals and are assumed to be ancient: 10,000 to 1 million years old (Barnes, 1966, Kemperman and Barnes 1976, Mitton and Grant 1996).

Regardless of origin (seedlings or suckers) aspen is rated as very intolerant of competition (USDA Forest Service, 1965). Thus even if moisture is not limiting for seedling germination, aspen needs a bare seedbed for successful germination and establishment.

After the Ice Age

There has been continuous climate change in the period preceding the retreat of the continental ice sheet and continuing to the present. Between 12,000 and 10,000 years BP, the ecological conditions were tundra like. This was the period when giant Pleistocene herbivores such as mammoths, muskoxen, camels and bison browsed on aspen, spruce and willow which colonized the bare land exposed
by the retreating ice. Around 10,000 years BP most of the Pleistocene megafauna became extinct. The reasons for this are not known, but over-hunting by the Clovis people, and climate change (the warming trend during the hypsithermal, and associated changes in vegetation) have both been put forward as possible explanations (Pielou, 1991, Hills, 2002).

The predominant reproduction through suckering in Alberta following aspen post-glacial re-colonization has not permitted genetic recombination and periodic sexual selection. This means that we would not expect to find development of distinctive locally adapted populations. There is molecular genetic evidence to support this hypothesis (Cheliak and Dancik, 1982, Jelinski and Cheliak, 1992). There is relatively little population genetic differentiation within Western Canada, but there is considerable variation from family to family, and likely between individuals within families (Li, 1995, Thomas et al. 1998). A preliminary provenance study in BC, Alberta and Saskatchewan also supports this idea. There is relatively little differentiation between ‘provenances’ in Alberta, but seed sources from Minnesota are consistently superior in their growth performance relative to local seedlots. (Brouard and Thomas, 2002). The non-optimality of local races was observed by Namkoong (1969) who argued that it may be a reflection of the difference between the reproductive fitness of an individual and the ‘fitness’ at meeting our growth and yield expectations.

The maladaptation hypothesis

The hypothesis presented here is that aspen populations are maladapted to their current growing environments. This is because clone patches are likely very old. They may have originated at the original re-colonization of bare land following deglaciation or during the warm and moist hypsithermal period. Even if some seedling regeneration has taken place subsequently, the frequency of sexual selection events is likely considerably lower than in a non-cloning species such as lodgepole pine (\textit{Pinus contorta} Douglas).

Lodgepole pine has been the subject of considerable genecological research (Rehfeldt et al. 1999). Interior lodgepole pine (\textit{P. contorta} subsp. \textit{latifolia} Engelm.) exhibits pronounced population differentiation. However even in this species with ample opportunity for genetic recombination and intense selection, there is a significant adaptational lag, with populations generally occupying colder climates and higher elevations than their optima as measured in provenance trials (Rehfeldt, 2000). Rehfeldt (2000) suggests that it is density-dependent selection rather than variation in the physical environment that is responsible for the steep clines.

It is clear; that in order to have survived for 7-10,000 years, the aspen clones cannot be completely mal-adapted. It is quite likely though that they are sub-optimally adapted, in the sense that in the absence of competing vegetation on a particular site we can usually find a different population that will survive and grow faster than the local one.
It can be argued that Alberta aspens are adapted to a fossil climate.

**A test of the hypothesis**

In Alberta, aspens commonly occur in association with other boreal hardwood species such as balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh.). These two species are also wind-pollinated and have small wind-dispersed seeds. They generally rely on seed based regeneration and have occupied the same habitats as aspen since the glacial retreat. It would be expected that local populations of these two species would have had some opportunity for genetic recombination and density dependent selection in the past 10-12,000 years. By establishing a provenance trial with materials from a range of local populations of the three species and testing them on contrasting sites, we would expect to observe more adaptational lag in aspen than in the other two species.

While this would only be an empirical test of the maladaptation hypothesis, the results would add to the body of evidence concerning geneecology and adaptation to a changing climate.

**Conclusions**

The clonal growth habit of aspen has an important influence on population differentiation. Climate change since post-glacial re-colonization has greatly reduced the opportunity for genetic recombination and selection in aspen. A better understanding of the degree of adaptational lag in aspen and clone transfer potentials is urgently required.

**Literature Cited**


